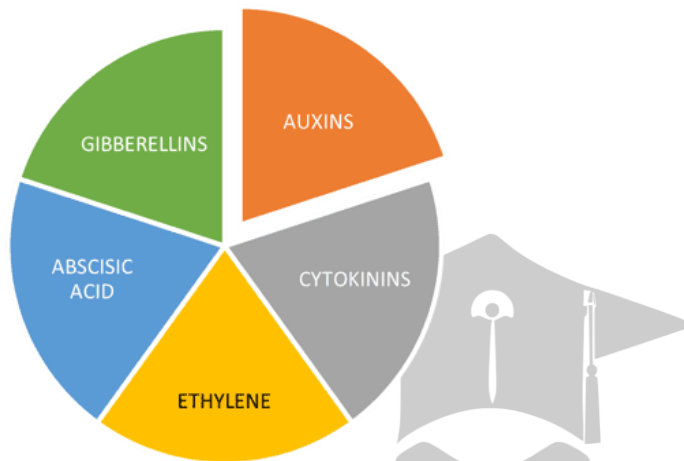


CSIR NET Life Science Unit 6

Plant Growth Regulators

Plants produce specific chemical substances that can move from one organ to the other and provide physiological control on growth. These substances, which are active in very small amounts, are called **plant hormones** or **growth regulators**.



1. AUXINS: Auxins (Greek, Auxein = to grow), isolated initially from human urine, were the first plant PGR discovered. The term auxin is applied to the indole-3-acetic acid (IAA) and other natural and synthetic compounds with certain growth-regulating properties. They are generally produced by the growing apices of the stems and roots, from where they migrate to the regions of their action.

(a) Biosynthesis: indole-3-acetic acid (IAA), the most important natural auxin in plants, is mainly synthesized from the amino acid tryptophan (Trp). The first chemical step of auxin biosynthesis is removing the amino group from Trp by the *Tryptophan Aminotransferase* to generate indole-3-pyruvate (IPA). IPA then undergoes oxidative decarboxylation catalyzed by the *Yucca* family of flavin monooxygenases to produce IAA.

(b) Transport: Auxin transport occurs in two distinct pathways: passive diffusion through the plasma membrane (PM) and active cell-to-cell transport, depending on the protonation state of IAA. A fraction of auxin in the acidic cell wall (pH 5.5) becomes protonated (IAAH), which can diffuse passively across the plasma membrane into the neutral cytosol (pH 7.0) and dissociates to its charged form (IAA⁻). The less permeable proton-dissociated IAA is trapped in the cytosol carrier proteins, which requires ATP; Hence, the process is active.

2. GIBBERELLINS: Gibberellins (GAs) are tetracyclic diterpenoid plant hormones that regulate many different aspects of plant growth and development through the entire life cycle of the plant.

(a) Biosynthesis: GAs are usually synthesized from higher plants' methylerythritol phosphate (MEP) pathway. In this pathway, bioactive GA is produced from trans-geranylgeranyl diphosphate (GGDP). MEP pathway is summarized as:

- i. GGDP is converted to ent-copalyl diphosphate (ent-CPD) by ent-copalyl diphosphate synthase
- ii. ent-CPD is converted to ent-kaurene by ent-kaurene synthase
- iii. ent-kaurene is converted to ent-kaurenol by ent-kaurene oxidase (KO)
- iv. ent-kaurenol is converted to ent-kaurenal by KO
- v. ent-kaurenal is converted to ent-kaurenoic acid by KO
- vi. ent-kaurenoic acid is converted to ent-7 α -hydroxykaurenoic acid by ent-kaurene acid oxidase (KAO)
- vii. ent-7 α -hydroxykaurenoic acid is converted to GA12-aldehyde by KAO
- viii. GA12-aldehyde is converted to GA12 by KAO. GA12 is processed to the bioactive GA4 by oxidations on C-20 and C-3, which is accomplished by 2 soluble ODDs: GA 20-oxidase and GA 3-oxidase.

Transport: The transport of gibberellins in plants is non-polar. Gibberellins have been found from both phloem and xylem exudates from a variety of plants. Gibberellin's transport may also occur in the xylem due to its lateral movement between the two vascular tissues, i.e., the xylem and phloem. The gibberellins are not translocated in plants as free molecules but probably in their bound form as gibberellins-glycosides.

3. CYTOKININS: The searches for natural substances with cytokinin-like activities led to the isolation of Zeatin from corn kernels and coconut milk, etc. Since the discovery of zeatin, several naturally occurring cytokinins, and some synthetic compounds, with cell division promoting activity, have been identified from plants.

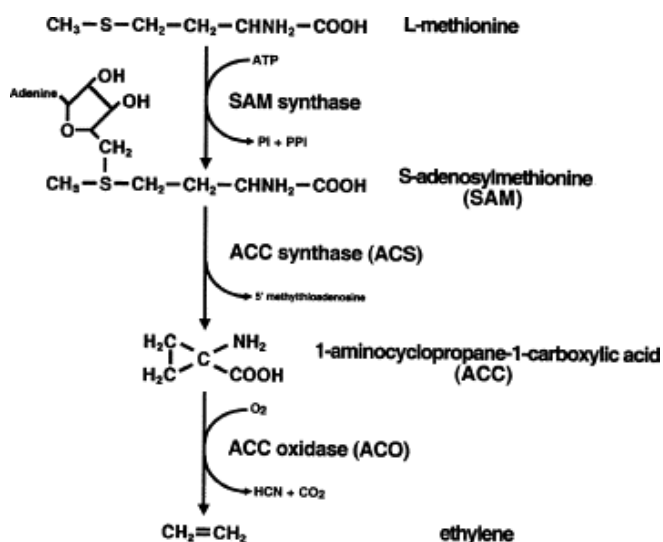
(a) Biosynthesis: The purine type of cytokinin is more clearly known than other types. The biosynthesis of purine nucleotide (purine base + ribose sugar + phosphate) began with the ribose phosphate, and the purine ring is built on it,

step by step. The first nucleotide to be synthesized by this process is inosine monophosphate (IMP). IMP is then converted to either guanosine monophosphate (GMP) or adenosine monophosphate (AMP). Next, free Cytokinins are synthesized from adenosine monophosphate (AMP) and isopentenyl pyrophosphate by the condensation reaction in the presence of the enzyme isopentenyl transferase. The product formed is N^6 (Δ^2 -isopentenyl) adenosine 5' monophosphate. The compound is supposed to be the precursor of all other Cytokinins. The N^6 (Δ^2 - isopentenyl)-adenosine 5' monophosphate is converted to N^6 (Δ^2 - isopentenyl)-adenosine by the removal of the phosphate by phosphatase and further converted to N^6 (Δ^2 -isopentenyl)- adenine, which is then hydroxylated from free zeatin. Reduction of the double bond in the isopentenyl side chain of zeatin would give rise to dihydrozeatin.

(b) Transport: The presence of cytokinins in the xylem sap proves that the hormone synthesized in roots moves upward in a polar fashion to the shoot and thereby regulates the plant's growth. Cytokinins are transported from the root to the shoot in the xylem as zeatin riboside. After reaching the leaves, some amount of these zeatin ribosides is either converted to the free base, which possesses hormonal activity or to cytokinin glucosides.

4. ETHYLENE: This is a simple gaseous PGR. It is synthesized in large amounts by tissues undergoing senescence and ripening of fruits.

(a) Biosynthesis: The ethylene biosynthetic pathway consists of a simple three-step catalytic conversion of L-methionine into ethylene. The first step is combining ATP and L-methionine into S-adenosylmethionine (SAM) by the enzyme methionine *S*-adenosyltransferase. SAM is subsequently converted to 1-aminocyclopropane-1-carboxylic acid (ACC), representing the first unique step of ethylene biosynthesis. The final step of ethylene biosynthesis is ethylene from ACC, which is catalyzed by the enzyme ACC oxidase (ACO).



(b) Transport: Due to its hydrophobic nature, ethylene can easily pass through the plasma membrane into the cell, easily diffuse within the plant or plant part and flushed out of plant tissues through intercellular spaces.

5. ABSCISIC ACID: Abscisic acid (ABA) is also called the stress hormone because hormone production is stimulated by drought, waterlogging and other adverse environmental conditions.

(a) Biosynthesis: Two pathways have been suggested for the biosynthesis of abscisic acid. One involves the cleavage of a C_{40} precursor, a xanthophyll carotenoid, and the other involves the direct formation from the C_{15} precursor, farnesyl pyrophosphate. In the Indirect or xanthophyll cleavage pathway of ABA, the biosynthetic pathway begins with the C_5 isoprene unit, isopentenyl pyrophosphate (IpPP), and through a few steps leads to the synthesis of oxygenated carotenoid like C_{40} xanthophyll, zeaxanthin, which is then converted to violaxanthin. Subsequently, violaxanthin is converted to 9-cis-neoxanthin, which undergoes cleavage to form the C_{15} compound xanthoxin, possibly outside the chloroplasts. Xanthoxin is a neutral growth inhibitor with ABA-like properties. In the last step, xanthoxin is converted to ABA aldehyde in the cytosol by losing the epoxy group, which is finally oxidized to ABA. This pathway is predominant in higher plants. On the other hand, a direct pathway for ABA biosynthesis has been suggested, which uses the initial steps of polymerization of isoprene units leading to the formation of a C_{15} precursor farnesyl pyrophosphate, a sesquiterpenoid molecule. The C_{15} ABA is directly synthesized from C_{15} farnesyl pyrophosphate. The direct pathway occurs mainly in the fungi.

(b) Transport: ABA can be transported over long distances in plants via the phloem and xylem, and the movement may occur from mature leaves to shoot tips and roots. ABA movement shows either a slight basipetal polarity or it is non-polar. ABA synthesized in the roots can be transported to the shoot via the xylem. ABA concentration in xylem sap of water-stressed plants rises several folds as compared to the well-watered plants. It has been noted that depending upon the increase in xylem sap pH, ABA undergoes redistribution in the leaf during water stress. Under normal conditions, the xylem sap is slightly acidic (pH 6.3), which is favourable for the mesophyll cells to take up an un-dissociated and protonated form of ABA. However, the xylem sap becomes slightly alkaline (pH 7.2) during water stress-causing dissociation of ABAH to free ABA. Since ABA does not readily cross the membrane and enter the mesophyll cells, more ABA is expected to reach the guard cells.

PHYSIOLOGICAL FUNCTIONS OF PGRs:

A. AUXINS

The primary physiological effect of auxin in plants is to stimulate the elongation of cells in the shoot. A prevalent example of this is phototropic curvatures, where unilateral light unequally distributes the auxin in the stem tip.

It has been a common observation in many vascular plants, especially the tall and sparsely branched ones, that if the terminal bud is intact and growing, the growth of the lateral buds just below it remained suppressed. Removal of the apical bud results in the rapid growth of the lateral buds. This phenomenon in which the apical bud dominates over the lateral buds and does not allow the latter to grow is called apical dominance. Auxin hormone is responsible for maintaining apical dominance.

Auxin can induce the formation of parthenocarpic fruits. In nature also, this phenomenon is not uncommon. In such cases, the concentration of auxins in the ovaries is higher than in the ovaries of plants which produce fruits only after fertilization. In the latter cases, the concentration of the auxin in ovaries increases after pollination and fertilization.

Besides cell elongation, the auxin may also be active in cell division. In fact, in many tissue cultures where the callus growth is quite normal, the continued growth of such callus takes place only after the addition of auxin.

Auxin induces vascular differentiation in plants. This has also been confirmed in tissue culture experiments and from studies with transgenic plants. Cytokinins are also known to participate in the differentiation of vascular tissues, and it is believed that vascular differentiation in plants is probably under the control of both auxin and cytokinins.

B. CYTOKININS

Cytokinins are essential for cytokinesis through chromosome doubling can occur in their absence. In the presence of auxin, cytokinins bring about division even in permanent cells. Cell division in callus (unorganised, undifferentiated irregular mass of dividing cells in tissue culture) requires both hormones.

Like auxin and gibberellins, cytokinins also cause cell elongation.

Both auxin and cytokinins are essential for morphogenesis or differentiation of tissues and organs. For example, buds develop when cytokinins are in excess, while roots are formed when their ratios are reversed.

The presence of cytokinin in an area causes preferential movement of nutrients towards it. When applied to lateral buds, they help in their growth despite the presence of apical bud. They thus act antagonistically to auxin, which promotes apical dominance.

Senescence is the phenomenon in which the mature leaves lose their pigment chlorophyll, turn yellow, proteins are degraded, and ultimately

they shed from the plant. Richmond and Lang (1957), while working on detached leaves of

Xanthium observed that the application of cytokinins delays the process of senescence for several days. The phenomenon of delaying senescence by application of cytokinins is known as Richmond- Lang effect.

C. GIBBERELLINS

1. Certain light-sensitive seeds, e.g., lettuce and tobacco, show poor germination in the dark. However, germination starts vigorously if these seeds are exposed to light or red light. This requirement of light is overcome if the seeds are treated with gibberellic acid in the dark.

2. In temperate regions, the buds formed in autumn remain dormant until next spring due to severe colds. This dormancy of buds can be broken by gibberellin treatment. In potatoes also, there is a dormant period after harvest, but the application of gibberellin sprouts the eyes vigorously.

- The most pronounced effect of gibberellins on plant growth is the elongation of the internodes, so much so that in many plants such as dwarf pea, dwarf maize etc., they overcome the genetic dwarfism. It is considered that in such dwarf plants, (i) the gene for producing gibberellin is missing, or (ii) the concentration of the natural inhibitors is higher. When external gibberellin has applied, the deficiency of the endogenous gibberellins is made good or the external gibberellin overcomes the effect of natural inhibitors, which fall short.
- 3.

- In many herbaceous plants, the early period of growth shows rosette-habit with short stems and cauline leaves. Under short days the rosette habit is retained, while under long days, bolting occurs, i.e., the stem elongates rapidly and is converted into floral axis bearing flower primordia. This bolting can also be induced by the application of gibberellin even under non-inductive short days.
- 4.

- Gibberellins stimulate germination of the pollen grains. Likewise, the growth of the fruit and the formation of parthenocarpic fruits can be induced by gibberellin treatment.
- 5.

D. ABSCISIC ACID

- The role of ABA in causing stomatal closure in plants undergoing water stress is now widely recognised. Various workers have suggested that in response to the water stress, the permeability of the chloroplast membranes of mesophyll cells to ABA is greatly increased.
- 1.

- Abscisic acid induces dormancy of buds towards the approach of winter.
2. Abscisic acid accumulates in many seeds during maturation and apparently contributes to seed dormancy.

- ABA acts as a general inducer of senescence (Thimann). The onset of
3. senescence is correlated with stomatal closure. The ABA content of ageing leaves increases markedly as senescence is initiated.

- In long-day plants, the effect of gibberellins on flowering is counteracted by ABA, which accumulated in the leaves during the short winter days. This ABA
4. acts as an inhibitor of flowering in long-day plants. On the other hand, ABA induces flowering in short-day plants.

- The GA-induced synthesis of α -amylase and other hydrolytic enzymes in
5. barley aleurone cells is inhibited by abscisic acid. This inhibition can be reversed by increasing the amount of GA supplied.

E. ETHYLENE

- Ethylene usually inhibits the elongation of stems and roots, especially in dicots.
1. When elongation is inhibited, stems and roots become thicker by enhanced radial expansion of cells.

- It aids in the ripening of climacteric fruits and the dehiscence of dry fruits.
2. Ethylene is used to induce artificial ripening of these fruits, e.g., Citrus, Apple, Mango, Banana, etc.

3. Rhizomes, corms, bulbs and other storage organs can be made to sprout early by exposing them to ethylene.

- Ethylene accelerates the abscission of leaves, stems, flowers and fruits.
4. However, at 1 ppm, ethylene prevents the opening of flower buds and causes 'sleep' disease in flowers that are already open, making their petals roll inward.

5. It stimulates flowering in Pineapple and related plants though in other cases, the gaseous hormone causes fading of flowers. The external supply of a minimal quantity of ethylene increases the number of female flowers and hence fruits in Cucumber (feminizing effect).



Mentor Guru